Ecological Engineering 114 (2018) 76–87

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Impact of rainfall regime on methane flux from a cool temperate fen depends on vegetation cover

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ARTICLE INFO

Article history:
Received 1 May 2017
Received in revised form 21 June 2017
Accepted 23 June 2017
Available online 28 June 2017

Keywords:
Wetland
Mire
Climate change
Carbon cycle
Rain
Rainfall exclusion
Plant functional type
Northern peatland
Methanogenesis
Carbon balance
Global warming potential

ABSTRACT

Climate change projections forecast an intensification of the precipitation regime for many regions of the globe, including central North America, with fewer, larger events interspersed between longer periods devoid of rain or snow. This shift has the potential to affect the carbon cycling of peatland ecosystems, including the flux of methane from the peat. We conducted a field manipulation experiment where irrigation treatments were used to simulate different seasonal rainfall regimes. The treatments were designed such that total seasonal rainfall was held constant but discrete event frequency and magnitude were altered between treatments in a poor fen in southern Ontario, Canada. The rainfall regime was controlled over three vegetation types: *Sphagnum capillifolium* (moss); *Carex oligoperma* (sedge); and *Chamaedaphne calyculata* (shrub). Decreasing rainfall frequency from thrice-weekly to bi-monthly [coupled with 6X increase in event intensity] led to significantly greater CH_4 flux from the moss and sedge communities in the latter third of the growing season. The shrub communities were unaffected by the changing rainfall regime. A companion lab mesocosm experiment revealed the control the fluctuating water table had on the CH_4 fluxes from the vegetation community, particularly from the moss communities. Overall, there were significantly greater CH_4 fluxes from all communities with increasing days since the previous rainfall event. As precipitation frequency decreases results of this study demonstrate the potential for increased CH_4 flux to the atmosphere from peatland areas dominated by *Sphagnum* and herbaceous species. Wetland restoration and creation projects should consider these effects on peatland carbon cycling and function.

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1. Introduction

Peatlands store 1/3rd of global terrestrial carbon yet cover only 3% of the earth's land surface (Limpens et al., 2008). This disproportionate importance to the global carbon cycle is due to water-logged surface soils maintaining anoxic conditions lowering rates of decomposition relative to gross primary production (Dise et al., 1993; Moore et al., 1994). The presence of high water tables and anoxic conditions also lead to high rates of carbon export in the form of dissolved organic carbon (DOC) (Waddington and Roulet, 1997; Blodau et al., 2004;) and in particular gaseous methane (CH_4) (Roulet et al., 1992; Bridgham et al., 2013). CH_4 is a more powerful greenhouse gas than carbon dioxide (CO_2); therefore, high CH4 emissions significantly contribute to the climate warming potential of peatlands. Rising air temperatures increase peatland evapotranspiration, potentially lowering the water table, which will lead to increased aerobic respiration and CO_2 flux to the atmosphere (Tarnocai, 2009). On the other hand the climate-induced lowering of the water table will also limit CH_4 production and efflux (Roulet et al., 1992; Strack and Waddington, 2007). While the response of peatland CH_4 emissions to changing temperatures (Christensen et al., 2003; Tarnocai, 2006; Turetsky et al., 2008) and water tables (Nykanen et al., 1995; Whalen, 2005; Moore et al., 2011) have been the focus of much research considerably less information is known about the impact on CH_4 fluxes due to changing temporal patterns of rainfall as a consequence of climate change.

Climate change projections for temperate and boreal North America and Eurasia predict larger but less frequent precipitation events (IPCC, 2013; Sillmann et al., 2013). Increased temperatures lead to higher evapotranspiration rates and atmospheric moisture content, increasing the intensity of precipitation events and the duration between events (Emori and Brown, 2005; Seneviratne et al., 2012). With a shift in precipitation regime to fewer events of greater intensity soil water dynamics are predicted to become more variable (Knapp et al., 2008). Research on the effects of pre-

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https://doi.org/10.1016/j.ecoleng.2017.06.047
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cipitation on methane fluxes is limited to changes in total rainfall amount. Field studies have noted that drier seasons have led to decreased emissions, while particularly wet seasons have increased methane efflux in peatlands (Bubier et al., 2005; Olson et al., 2013; Yang et al., 2014). This is likely due to corresponding changes in the water table. However, studies that have looked at CH_4 flux under low water table position have found that rainfall events led to increases in CH_4 efflux due to the degassing of sub-surface peat (Kettunen et al., 1996; Shoemaker et al., 2012). Other studies (Romanowicz et al., 1993; Glaser et al., 2004) have found that long periods of no precipitation on to peatlands resulted in significant increases of CH_4 efflux due to depressurizing of sub-surface peat. These studies suggest that longer rainless periods interspersed with large events could lead to increased CH_4 emissions in peatlands, but this question remains to be explored.

The role of precipitation on peatland carbon dynamics has most often been explored from an annual or seasonal perspective (Alm et al., 1999; Laiho et al., 2003; Fenner and Freeman, 2011). Bragazza et al. (2016) found that lowered annual precipitation leads to lower carbon accumulation rates in peatlands. However, Waddington and Roulet (2000) suggest the variability of precipitation events may exert a stronger control than total seasonal amounts on peatland carbon. Small (<1 mm) precipitation inputs have been shown to increase *Sphagnum* productivity in peatlands (Strack and Price, 2009; Adkinson and Humphreys, 2011). In a controlled mesocosm experiment, Nijp et al. (2014) found that decreasing the frequency of rainfall events over *Sphagnum* led to greater CO_2 emissions despite all mesocosms receiving the same total rainfall amounts. Despite the apparent importance of short-term droughts, small precipitation inputs, and rainfall timing to carbon cycling in peatlands there is a dearth of knowledge of the direct effects of varying rainfall return periods within a growing season on CH_4 flux from peatlands.

This study aims to quantify the effect of changing the frequency of rain events on CH_4 flux from a cool temperate poor fen. Elucidation of the response, and the environmental controls of the response, will aid land managers and inform land-atmosphere climate models on the role of peatlands in the global carbon cycle. Peatland CH_4 emissions can vary by several orders of magnitude from site to site and even within sites due to the presence of different vegetation (Dise, 1993; Bridgham et al., 2013; Turetsky et al., 2014). We applied our rainfall frequency treatments on representatives of the three dominant plant functional types in poor fens and bogs: *Sphagnum* moss, herbaceous sedge, and ericaceous shrubs. Our specific objectives were 1) to determine the effect of changing rainfall frequency on the flux of CH_4 from the three vegetation communities, and 2) to examine the interaction of the applied rainfall regimes with relevant environmental variables, particularly the fluctuation in the water table. We addressed these objectives through experimentation in the field through the construction of rainout shelters as well as lab manipulation on peat mesocosms.

2. Methodology

2.1. Study site

The field manipulation study was carried out in a portion of a 130 ha undisturbed poor fen (44°15′13.34″N, 80°20′46.83″W) in southern Ontario, Canada. Peat depth throughout the study area averages 2.1 m, and is underlain by sandy silt till (Burwasser, 1974) over dolomite of the Guelph formation. The climate for this region is cool temperate, with a mean annual temperature and precipitation of 6.4 °C and 996 mm, respectively (1981–2010 normal at Ruskview, ON station, data available: http://climate.weather..gc.ca/climate_normals/). In the period of May-October (inclusive), the mean temperature is 15.1 °C and mean precipitation is 517 mm, with rainfall (>0.2 mm) occurring on 43% of the days throughout the growing season.

The peatland vegetation mainly consisted of a relatively continuous carpet of *Sphagnum capillifolium*, *S. rubellum*, *S. fuscum* and *S. magellacicum*. Vascular vegetation covered about 75% of the ground in distinct patches, and was equally dominated by sedges and ericaceous shrubs. The sedge species included *Carex oligosperma* and *Eriophorum vaginatum*, and ericaceous shrubs species including evergreen *Chamaedaphne calyculata*, *Rhododendron groenlandicum* and deciduous shrub *Vaccinium uliginosum*. *Sphagnum* ground cover was ~100% in the sedge-dominated areas, but was relatively sparse (averaging 15% ground cover) in the areas with mature shrubs. More detail on site characterization can be found elsewhere (Radu, 2017).

2.2. Field experimental design

We established a full-factorial field experiment to examine the effect of different rainfall regimes on CH_4 flux among different peatland vegetation communities. The total seasonal rainfall was held constant between rainfall regime treatments and rainfall event frequency was decreased between the three treatments with corresponding increases in rainfall intensity of each event. 27 sample plots were randomly distributed among the dominant plant communities in the peatland: 1) *Sphagnum* moss (mainly S. *capillifolium*) (hereafter referred to as Moss plots) 2) *Sphagnum* with sedges (mainly *Carex oligosperma*) (Sedge plots), and 3) *Sphagnum* with ericaceous shrubs (mainly *C. calyculata*) (Shrub plots). The 9 plots within each community were assigned one of three rain frequency treatments (Table 1), replicated three times. The plots were 9.3 m^2 and spaced at least 10 m apart within a 3000 m^2 study area.

To implement the irrigation treatments, we built fixed-location rainout shelters to block natural precipitation from the vegetation plots throughout the study period. The shelter scaffolding was built the summer prior to field sampling. Rainout shelters were covered with 6 mil transparent polyethylene sheeting (Uline, Brampton, Ontario, Canada). The shelter roofs were found to transmit 90% of incoming solar radiation and exclude 98% of precipitation. The sides of the shelters were left uncovered to minimize effects on the microclimate. Further details of the design and efficiency of the rainout shelters can be found elsewhere (Didiano et al., 2016). Trenches (30 cm deep) were dug around the perimeter of each shelter and lined with reinforced polyethylene sheeting to limit the lateral flow of water between the sample plots and the surrounding peatland.

We tested three rain frequency treatments on the peatland vegetation: 3 events/week (hereafter referred to as “High-Frequency”), 1 event/week (“Medium-Frequency”), and 1 event/2 weeks (“Low-Frequency”). Natural rainwater captured throughout each week was used to water the plots for the following week (or 2 weeks for the Low-Frequency treatment). This resulted in varying amounts of water applied each week depending on the natural precipitation regime. The duration of each irrigation treatment was held constant at 0.5, one, and two hours for the High-, Medium-, and Low-Frequency treatments, respectively, regardless of irrigation amount, and average irrigation event intensity is expressed on a daily scale. Although the *frequency* of the rain events was different, the total *amount* of water in each 2-week period was equal between all treatments.

2.3. Methane sampling and environmental variables

CH_4 fluxes were measured at least weekly from the plots throughout the study period (01- June–12-September 2015) at midday (1000–1700 h) using the dynamic closed chamber method

Table 1
Rainfall regime of study period (June–September 2015) and rainfall treatments applied in the field and the lab.

Location	Irrigation Frequency Treatment	Event Frequency (X/week)	Period between rain events (days)	Event Intensity (mm/day)	Proportion of study period with rain (% of days)	Total Rainfall (mm)
Field	Natural	3 (±2)	2 (±2)	6 (±9)	38	199
	High	3	1 (±1)	5 (±2)	42	173
	Medium	1	6 (±1)	13 (±6)	14	173
	Low	0.5	13 (±1)	29 (±8)	7	173
Lab	High	3	1.33	2.3	42	166
	Medium	1	6	6.9	14	166
	Low	0.5	13	13.8	7	166

(Alm et al., 2007). Three grooved, square-shaped aluminum collars (60 × 60 cm) were installed to a depth of 20 cm in each vegetation-rainfall treatment plot two months prior to the measurement campaign. During each measurement period four gas samples were collected over 21 min from an opaque PVC chamber placed over the collars sealed from the atmosphere with water in the collar grooves. A fan was mounted on the inside of the chamber to mix the air and homogenize the CH_4 concentration during measurements. Samples were stored in pre-labelled, evacuated 15 mL Exetainers (Labco Ltd., UK) until analysis on an SRI Greenhouse Gas GC. We used the convention that negative numbers denote ecosystem CH_4 uptake and positive numbers denote ecosystem CH_4 loss to the atmosphere.

To monitor environmental variables that affect CH_4 exchange, a meteorological station was installed at the center of the study site. Air temperature and relative humidity were recorded with a HC2-S3-L probe (Campbell Scientific, Utah, USA) and soil temperature at depths of −50, −20, −10, −5, 0 and +5 cm relative to ground surface was measured with thermocouple wire inserted into the substrate. These data were measured every 10 s and averaged over 30 min periods by a CR1000 data logger (Campbell Scientific, Utah, USA). Precipitation was recorded automatically using a HOBO tipping bucket rain gauge (Onset Computer Corporation, Massachusetts, USA).

Water table depth in each sample plot was measured in 2.54-cm diameter fully perforated PVC wells covered with 250-μm Nitex mesh inserted to a depth of 1 m. Soil moisture was measured for each vegetation-rainfall treatment with EC-5 sensors (Decagon Devices Inc., Washington, USA) inserted vertically into the peat for a composite depth of 0–5 cm. Data were measured at half-hourly intervals with EM50 data loggers (Decagon Devices Inc.). Soil temperature at depths of −50, −20, −10, −5, 0 and +5 cm was measured within each sample plot using thermocouple wires inserted into the peat and a handheld portable Comark thermometer (Cole-Parmer Canada, Quebec, Canada).

2.4. Laboratory experiment collection and setup

We conducted a companion laboratory study to better control environmental conditions other than rainfall frequency and magnitude. In June 2015, intact peat cores (30 cm diameter × 40 cm height) were collected from areas in the poor fen near the field study. Sampling locations were chosen within a 50 m^2 area such that cores represented each of the three dominant species assemblages at the peatland: 1) mosses only (*S. capitifollium*), 2) mosses with sedges (*S. capitifollium* with *C. oligosperma*), and 3) mosses with ericaceous shrubs (*S. capitifollium* with *C. calyculata*). Vegetation remained intact; however, for the Shrub cores it was only possible to obtain cores with small shrubs (~10 cm in height at time of collection) due to the horizontal growth pattern of the roots. Details on the core collection can be found elsewhere (Radu, 2017).

Cores were placed inside a growth chamber (FXC-19 Chamber, BioChambers, Winnipeg, Manitoba, Canada) to acclimate to the new environmental conditions for a 2-month period prior to measurement. Water levels were kept constant at −5 cm until the experiment began. The cores will hereafter be referred to as the 'Moss', 'Moss + Shrub,' and 'Moss + Sedge' mesocosms. Climate conditions within the chamber were programmed to vary through the day and night to simulate study site conditions during the 2015 growing season). Maximum photosynthetic photon flux density (PPFD) reached 450 μmol m^{-2} s^{-1}, and a fan circulated the air within the chamber. Most growth chamber experiments do not exceed the chosen PPFD level in the present study to avoid burning *Sphagnum* capitula (McNeil and Waddington, 2003; Strack and Price, 2009; Nijp et al., 2014).

2.4.1. Laboratory experimental design and measurement

Three precipitation frequency treatments were randomly assigned to mesocosms of each vegetation community type: 3 events/week ("High-Frequency"), 1 event/week ("Medium-Frequency"), and 1 event/2 weeks ("Low-Frequency"). The mesocosms were evenly watered with a diluted Rudolph nutrient solution (Rudolph et al., 1988; Faubert and Rochefort, 2002) to limit detrimental effects to *Sphagnum* moss growth (Dieleman et al., 2015). Rainfall treatment details are provided in Table 1. At the beginning of the study period, all water levels were set to −5 cm ('High') and after 2 months were adjusted to −15 cm ('Medium') by removing or adding water through the wells with a pipette. After another 2-month period water levels in each mesocosm were set to −25 cm (Low). Within each of these 2-month periods, WT positions were allowed to naturally fluctuate with the addition of rainwater and the loss of water through ET.

Measurements of WT levels were made thrice-weekly in 1.27-cm diameter PVC wells in each mesocosm. Volumetric moisture content (VMC) was measured as in the field. Mesocosms were sampled for CH_4 emissions using a 40-cm tall opaque cylindrical chamber throughout the study period between 1200 and 1700 h during simulated midday field conditions (air temperature = 21.0° C; relative humidity = 60%; maximum photosynthetic photon flux density (PPFD) = 450 μmol m^{-2} s^{-1}). A fan was mounted on the inside of the chamber to mix the air and homogenize the CH_4 concentration during measurements. During each measurement period, the chamber was fitted to a depth of 4 cm in the mesocosm and sealed with petroleum jelly. Gas samples were collected following the same procedure as in the field.

2.5. Statistical analysis

Differences in CH_4 efflux between rainfall frequency treatments, vegetation communities, and portion of the growing season were assessed with three-way ANOVA for the field data and two-way ANOVA for the lab data (where growing season partitioning was not done). Water table differences between rainfall treatment for each vegetation community and portion of the growing season were assessed with one-way ANOVA. Post-hoc pairwise comparisons of the mean responses to different treatments were assessed with Tukey tests. Linear and nonlinear regression analyses were performed between CH4 flux and measured environmental variables and the best, statistically valid fits are presented. All data were

tested a priori for normality using the Shapiro-Wilk test; data not meeting this criterion were log-transformed prior to analysis. All statistical analyses were performed using the Statistica 8 software package (StatSoft Inc.).

3. Results

3.1. Seasonal rainfall

A total of 199 mm of rain fell on the field study area over the sampling period. We were able to capture 87% of this ambient precipitation off our rainout shelters to apply to our treatments (Table 1). A 31-mm event on 12-June and a 41-mm event on 02-August exceeded the capacity of our rain barrels. The frequency of our High-Frequency treatment matched well with the mean return period of 3 events per week that occurred naturally; as did the mean depth of water applied to each treatment. In order to maintain the same total amount of rainfall applied to all three treatments over the study period the average depth of rain applied in the Medium-Frequency and High-Frequency treatments was twice and five-times the mean ambient event depth, respectively. Lab mesocosm frequency was controlled to mimic the field conditions. Event depths in the lab mesocosms were lower than ambient conditions to reflect the lack of drainage and lateral flow possible in the field.

3.2. Methane flux

Methane flux from the field treatments varied throughout the study period, with general increases in rates as the growing season progressed (Fig. 1). This was most pronounced in the Low-Frequency treatments of the Moss and Sedge communities, where CH_4 flux rates ranged from 14 to 15 mg C m^{-2} d^{-1} at the start of the study period to 33–35 mg C m^{-2} d^{-1} at the end of our collection period. Rates of CH_4 flux increased in the High-Frequency treatment in the Moss community and Medium-Frequency treatment of the Sedge community for the first half of the study period but decreased through the latter portion of the growing season. Some treatment – vegetation combinations had little change in fluxes through the growing season, such as the High-Frequency rain treatment in Sedge plots, where fluxes were between 10 and 20 mg C m^{-2} d^{-1} throughout the study period. Throughout the growing season CH_4 fluxes in the Moss, Sedge, and Shrub communities were 17.7 ± 17, 15.1 ± 6, and 6.2 ± 6 mg C m^{-2} d^{-1}, respectively, in the High-Frequency treatment, which most closely represented the return period and mean event depth of the ambient conditions at the study site.

There were significant differences in CH_4 fluxes between rainfall frequency, vegetation community, the period of measurement, and their interaction in the field (Table 2). Results of the three-way ANOVA revealed a stronger effect of vegetation type and period of growing season (early, middle, and late) than the irrigation frequency treatment. For all vegetation types the High-Frequency rainfall treatment did not significantly differ from both decreasing frequency treatments in the beginning of our measurement period; thus, there was not a systemic bias in our experimental design between rainout structure location or collection plots (Fig. 2). On the other hand, as the growing season progressed, differences in CH_4 flux between rainfall treatments were apparent in both Moss and Sedge plots, with significant differences in fluxes between High-Frequency and Medium-Frequency rain treatments in Moss and High-Frequency and both Medium-Frequency and Low-Frequency treatments in the Sedge communities. In the latter third of the growing season the effect of increasing duration between rain events on CH_4 flux in the Moss community became more pronounced, as mean flux rates increased two- and three-fold from 9.9 mg C m^{-2} d^{-1} in the High-Frequency treatment to 23.6 and 33.4 mg C m^{-2} d^{-1} in the Medium-Frequency and Low-Frequency rain treatments, respectively. A similar effect was found in the Sedge plots in the Late growing season, with mean rates ranging from 16.1, 21.7, to 28.6 mg C m^{-2} d^{-1} in the High-Frequency, Medium-Frequency, and Low-Frequency treatments, respectively. There were no significant differences in field CH_4 flux between irrigation treatments during the measurement period in the Shrub community.

The lab mesocosms allowed us to measure CH_4 flux from the different vegetation under changing rainfall treatment while controlling other environmental variables. Fluxes from the lab mesocosms were much higher than we found in the field, with values in the Moss and Moss + Shrub cores frequently above 300 mg C m^{-2} d^{-1} (Fig. 3). There were no apparent differences between rainfall treatments for each of the vegetation types during the first four weeks of measurement. Methane fluxes from the Medium- and Low-Frequency treatments were generally higher than the High-Frequency treatment in the Moss and Moss + Shrub cores after the water table was set to −15 cm at the four-week mark of the experiment (Fig. 3); however, when the water table was reset to −25 cm at the eight-week mark these differences tapered off concurrent with overall lower emissions.

Overall there were significant differences in CH_4 fluxes in the lab mesocosms between rainfall frequency and vegetation treatments, and their interactions (Table 3). Mean CH_4 flux from the Low-Frequency rainfall treatment was significantly higher than either the High- or Medium-Frequency treatment in the Moss mesocosms; both Low- and Medium-Frequency treatments had significantly higher mean rates of CH_4 emission than the High-Frequency treatment in the Moss + Shrub treatment (Fig. 4). There were no significant differences in between rainfall treatments in the Moss + Sedge mesocosms.

3.3. Water table fluctuation

The water table in the field was generally closest to the surface in the moss plots and decreased for all vegetation communities throughout the growing season (Table 4). Throughout the growing season there were generally no differences in water table position between the rain treatments in either the moss or shrub plots. In the sedge communities the water table under the areas selected to receive the High-Frequency treatment was naturally lower than the areas that received the Medium- and Low-Frequency treatments. This persisted throughout the growing season, with the water table in the High-Frequency treatment areas being on aver-

Table 2
Results of three-way ANOVA of methane flux in the field between rainfall frequency, vegetation communities, time of season, and their interactions.

Source	DF	F-Score	P value
Rainfall Frequency	2	16.099	<0.001
Vegetation Community	2	127.829	<0.001
Time of Season	2	50.996	<0.001
Frequency X Vegetation	4	12.861	<0.001
Frequency X Season	4	9.941	<0.001
Vegetation X Season	4	3.484	0.008
Freq X Veg X Season	8	7.492	<0.001

Table 3
Results of two-way ANOVA of methane flux from the lab mesocosms between rainfall frequency and vegetation communities, and their interaction.

Source	DF	F-Score	P value
Rainfall Frequency	2	8.501	<0.001
Vegetation Community	2	18.754	<0.001
Frequency X Vegetation	4	3.385	0.01

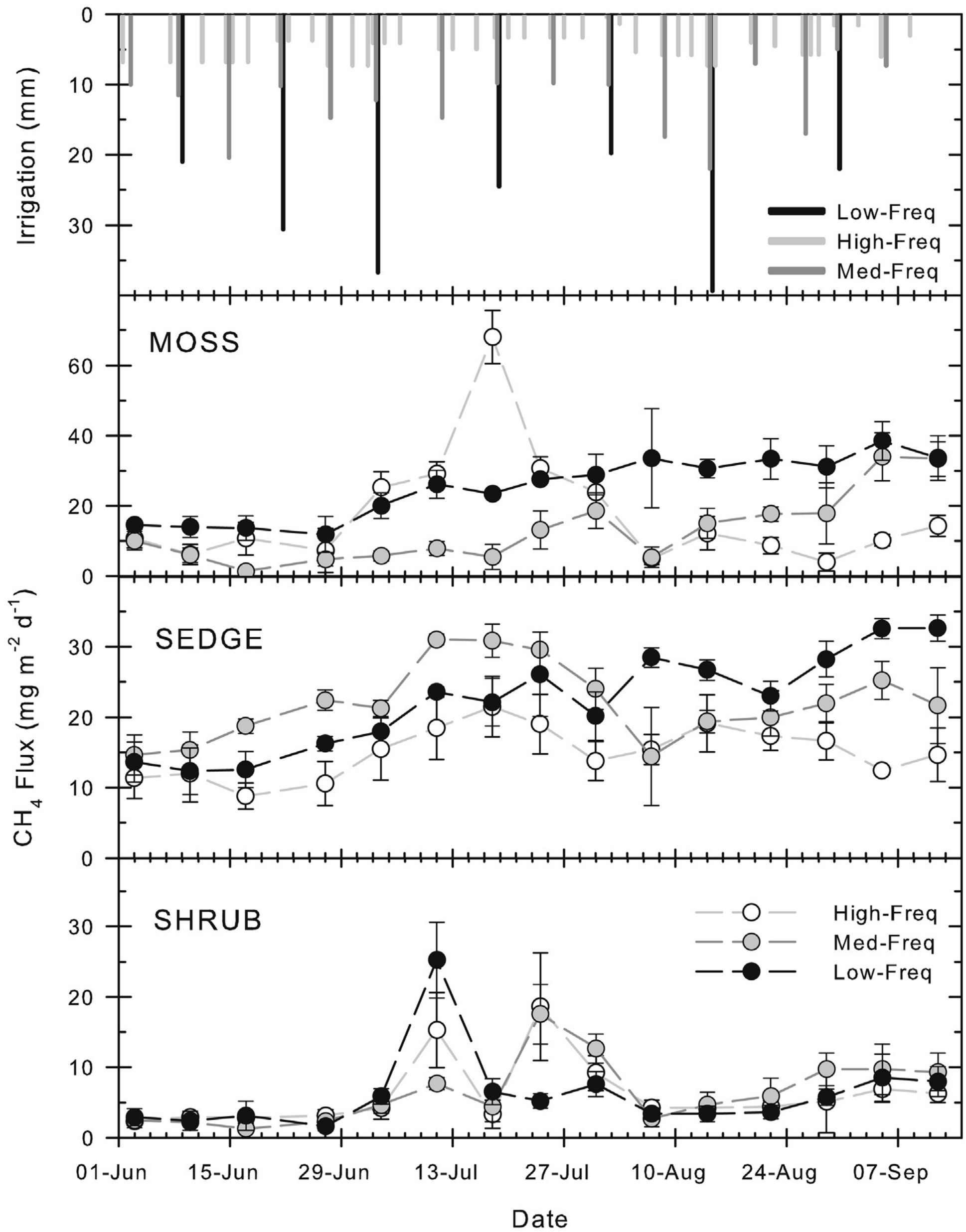

Fig 1. Time series of CH_4 flux from vegetation communities in the field in response to changing rainfall frequency.

Table 4
Water table position in the field grouped by portion of the growing season, vegetation community, and rainfall treatment. Values are means (± standard deviation).

Vegetation	Rain Treatment	Growing Season Water Table Depth (cm)		
		Early	Middle	Late
Moss	High Frequency	−8.4 (±1.7)	−14.9 (±3.3)	−23.7 (±3.9)[a]
	Medium Frequency	−6.8 (±3.2)	−10.9 (±4.7)	−17.6 (±4.1)[b]
	Low Frequency	−8.7 (±4.5)	−12.6 (±5.3)	−19.5 (±4.7)[ab]
Sedge	High Frequency	−14.9 (±3.0)[a]	−18.9 (±4.4)[a]	−26.7 (±3.6)[a]
	Medium Frequency	−3.7 (±2.7)[b]	−10.1 (±4.8)[b]	−17.9 (±3.8)[b]
	Low Frequency	−7.0 (±3.8)[c]	−11.1 (±5.2)[b]	−19.7 (±4.6)[b]
Shrub	High Frequency	−10.9 (±2.6)	−17.3 (±4.8)	−24.5 (±3.1)
	Medium Frequency	−12.1 (±2.4)	−16.0 (±5.1)	−24.8 (±3.0)
	Low Frequency	−11.3 (±4.8)	−15.1 (±5.5)	−20.9 (±7.2)

Superscripts refer to significant differences ($p < 0.05$) between rainfall treatments within a portion of the growing season for a vegetation community.

age ~7 cm lower than in the other two treatment areas of the sedge community (Table 4). As irrigation frequency decreased and event magnitude increased between the rain treatments the water table fluctuation increased, with increasing standard deviations around the mean position. For example, during the first several weeks of our measurement period the standard deviation nearly tripled in the moss plots between High- and Low-Frequency treatments.

The controlled conditions of the lab mesocosms revealed greater differences in the progression of the water table between rainfall treatments, particularly in the Moss + Sedge and Moss cores (Fig. 5). Despite receiving equal depths of water over a four-week period there was an 8 cm difference in water table position between Low- and High-Frequency treatments in the Moss mesocosms. The differences in water table depths were up to 10.2 cm between these treatments prior to the twice-monthly watering in the Low-Frequency treatment near the end of the experiment. There was no difference in water table position between the High-Frequency

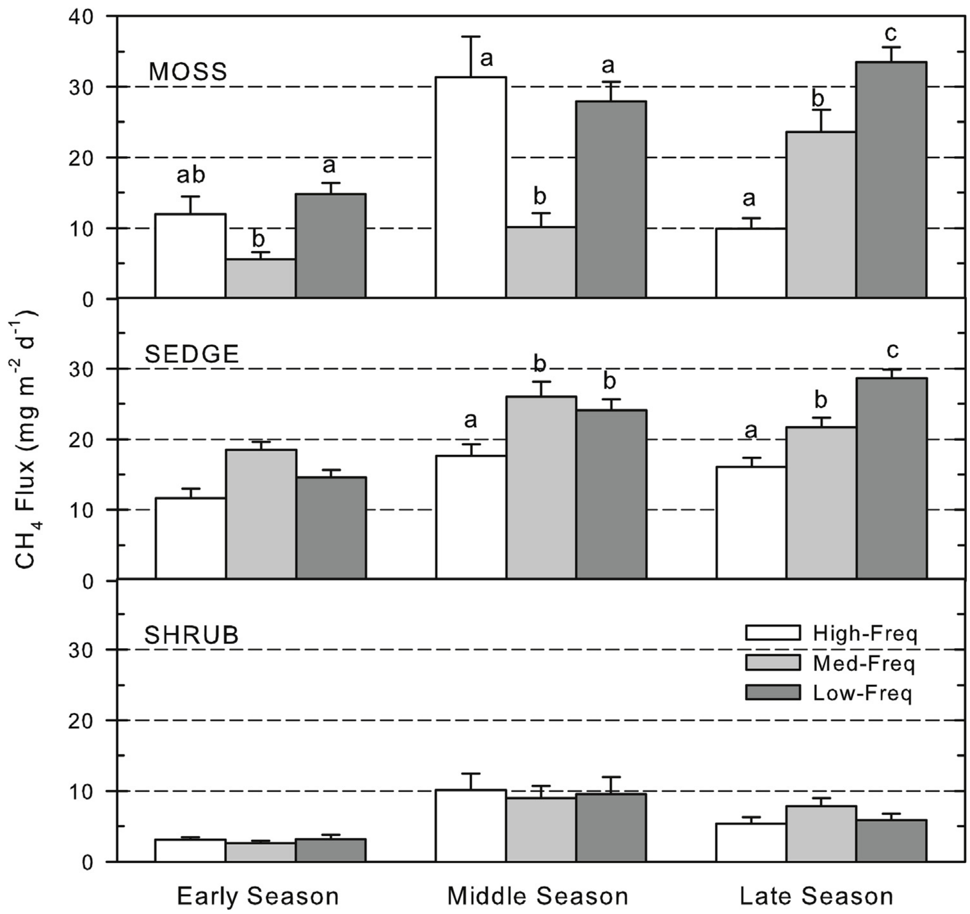

Fig. 2. Intra-seasonal CH_4 flux from vegetation communities in response to changing rainfall frequency from the field. Bars represent mean values (±standard error). Letters represent significant differences ($p < 0.05$) between rainfall treatments within a vegetation community and portion of the respective growing season.

and Medium-Frequency treatment in the Moss mesocosms for the duration of the lab experiment.

The differences in water table position between the three rainfall treatments were most apparent in the Moss + Sedge mesocosms (Fig. 5). After 39 days of the experiment the water table depths in the High-, Medium-, and Low-Frequency treatments were −20, −16.9, and −36.5 cm, respectively; the watering events on day 40 caused a 22.5 cm rise in water table in the Low-Frequency treatment, and brought the water tables to within 3.5 cm amongst the three treatments. Within 16 days of setting the water table to −15 cm in all cores the water table fell below the bottom of the cores (−40 cm) in the Low-Frequency treatment of the Moss + Sedge mesocosms, where it remained until it was reset to −25 cm on day 112. The water table of the High-Frequency treatment fell below this level on day 108, then again on day 128 following the water table reset. This dramatic water table fall was not observed in the Medium-Frequency treatment of the Moss + Sedge mesocosm. The Low-Frequency treatment only had minimal effect on relative water table position in the Moss + Shrub cores, and by the end of the experiment the water table was 4.5 cm lower in the High- versus Low-Frequency cores (Fig. 5).

3.4. Rainfall – water table interaction on methane flux

There were no significant correlations between rainfall treatment in any of the vegetation communities and most of the measured environmental variables (data not shown). Combining all data did reveal a highly significant moderate negative nonlinear relationship between water table depth and the CH_4 fluxes from the Moss plots (Fig. 6). Methane fluxes peaked when the water table was 23 cm below ground surface, and decreased as the water table was closer to the surface. There was also a significant exponential correlation between CH_4 emissions from all rainfall treatments in the Shrub and Sedge community ($R^2 = 0.34$, $p < 0.0001$; $R^2 = 0.10$, $p < 0.01$, respectively) with air temperature.

The water table in the field remained above −30 cm for the duration of the study period; thus, we were unable to explore the relationship between rainfall frequency and water table depth beyond this point. The lab experiment was designed to allow the water table to fall to −40 cm depth. Seven of nine vegetation–frequency treatment factors resulted in significant relationships between CH_4 flux and water table position (Fig. 7); all were nonlinear. In contrast to the field data, there was a slight exponential correlation between increased CH_4 flux and increasing water table position in the Moss lab mesocosms under High-Frequency irrigation. There was a Gaussian relationship between water table position and CH_4 flux for Moss under Low-Frequency and Moss + Shrub under Medium- and Low-Frequency. Peak CH_4 fluxes were found at water tables of −22.2, −20.0, and −21.9 cm in the Moss – Low-Frequency, Moss + Shrub – Medium-Frequency, and Moss + Shrub – Low-Frequency mesocosms, respectively. Moss + Sedge mesocosms had moderate to strong exponential or quadratic increases in CH_4 with increasing water table positions in all rainfall frequency treatments that were all highly significant (Fig. 7).

Methane fluxes from all vegetation treatments were significantly correlated with days since the last watering event (Fig. 8). There was a linear increase in fluxes measured the day following

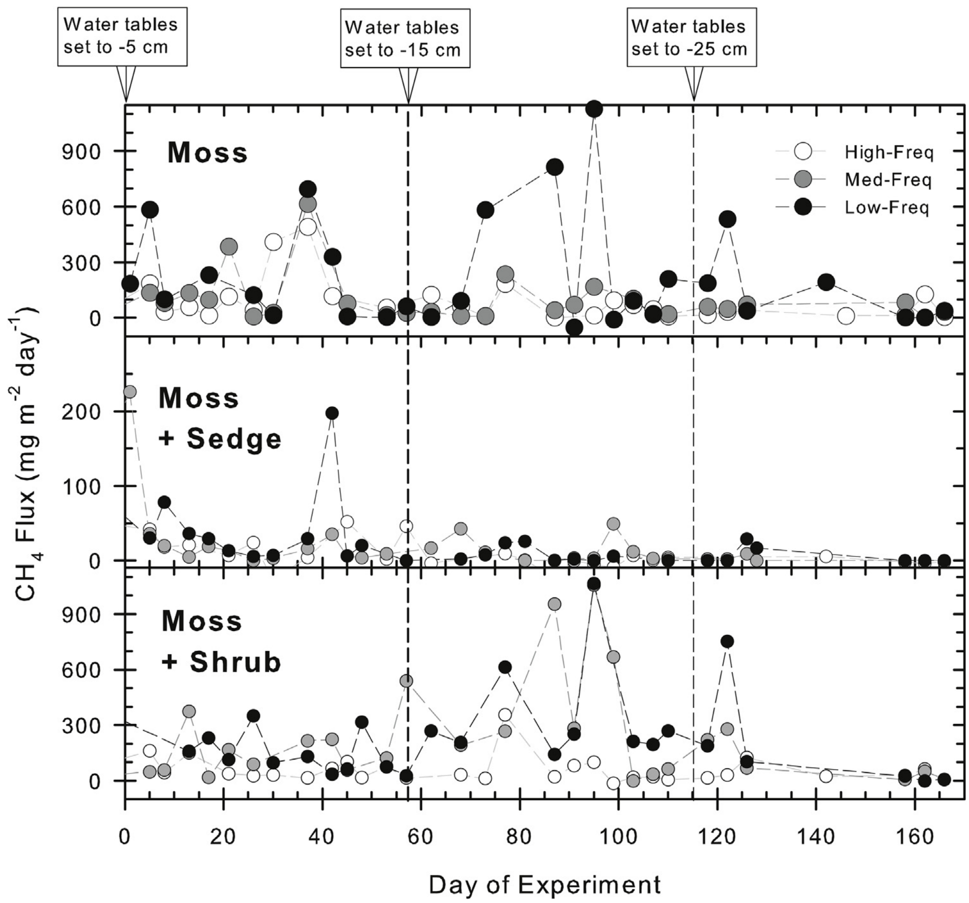

Fig. 3. Time series of CH_4 flux from vegetation communities in the lab mesocosms in response to changing rainfall frequency. Instances of manually setting the water table levels in all mesocosms to −5, −15, and −25 cm below surface are indicated.

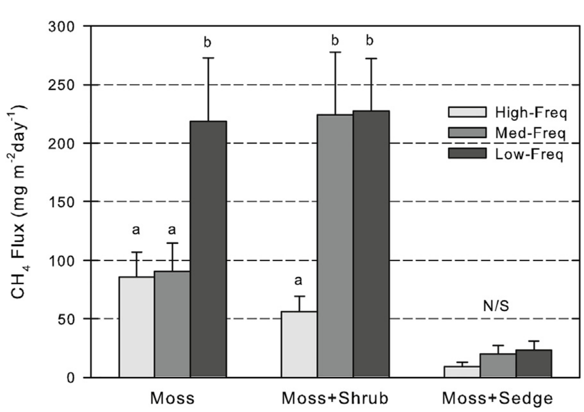

Fig. 4. CH_4 fluxes from vegetation communities in response to changing rainfall frequency from the lab mesocosms. Bars represent mean values (±standard error) for the duration of the lab experiment. Letters represent significant differences ($p < 0.05$) between rainfall treatments within a vegetation community.

a rainfall event with increasing length of time between rainfall events. This relationship was most pronounced in the Moss mesocosms. Water table position had some influence on this observed relationship, with deviations from the general linear increase depending on water table depth at time of measurement (Fig. 7). For example, in the Moss mesocosms the relationship was much steeper with water tables >−10 cm and a breakdown of this trend when the water table was between −10 and −20 cm. In the Moss + Shrub mesocosms when the water table was between −10 and −20 cm in depth higher CH_4 fluxes were observed six days since previous rain compared to >10 days between events.

4. Discussion

4.1. Rainfall regime effects on methane flux

The results of this study clearly show that a change in the rainfall regime during a growing season alters the flux of CH_4 from poor fens. Significant differences in CH_4 flux were found between the rainfall frequencies applied to the vegetation communities in both field and lab settings (Tables 2 and 3). The repackaging of rainwater into one larger event every two weeks rather than smaller events every three days led to greater CH_4 fluxes in the field in the Moss and the Sedge vegetation treatments in the latter portion of the growing season (Fig. 2). These differences were not apparent in the early growing season, demonstrating that these differences in CH_4 flux are not directly caused by the rainfall treatments (in which case the high-magnitude and intensity events of the Low-Frequency treatments would have resulted in significantly higher CH_4 fluxes early in the growing season as well). Rather, it is likely that the additive effects of infrequent rain of larger magnitudes throughout the season result in shifts in the physical and biochemical environment that promotes the production (or limits the oxidation) and release of CH_4 at some later point in the growing season.

In the lab higher CH_4 fluxes associated with the larger-magnitude, less frequent events were found in the Moss and Moss + Shrub treatments (Fig. 4). While there were juvenile shrubs in the Moss + Shrub mesocosms we were unable to collect any cores with mature shrubs and their roots intact. The shrubs collected

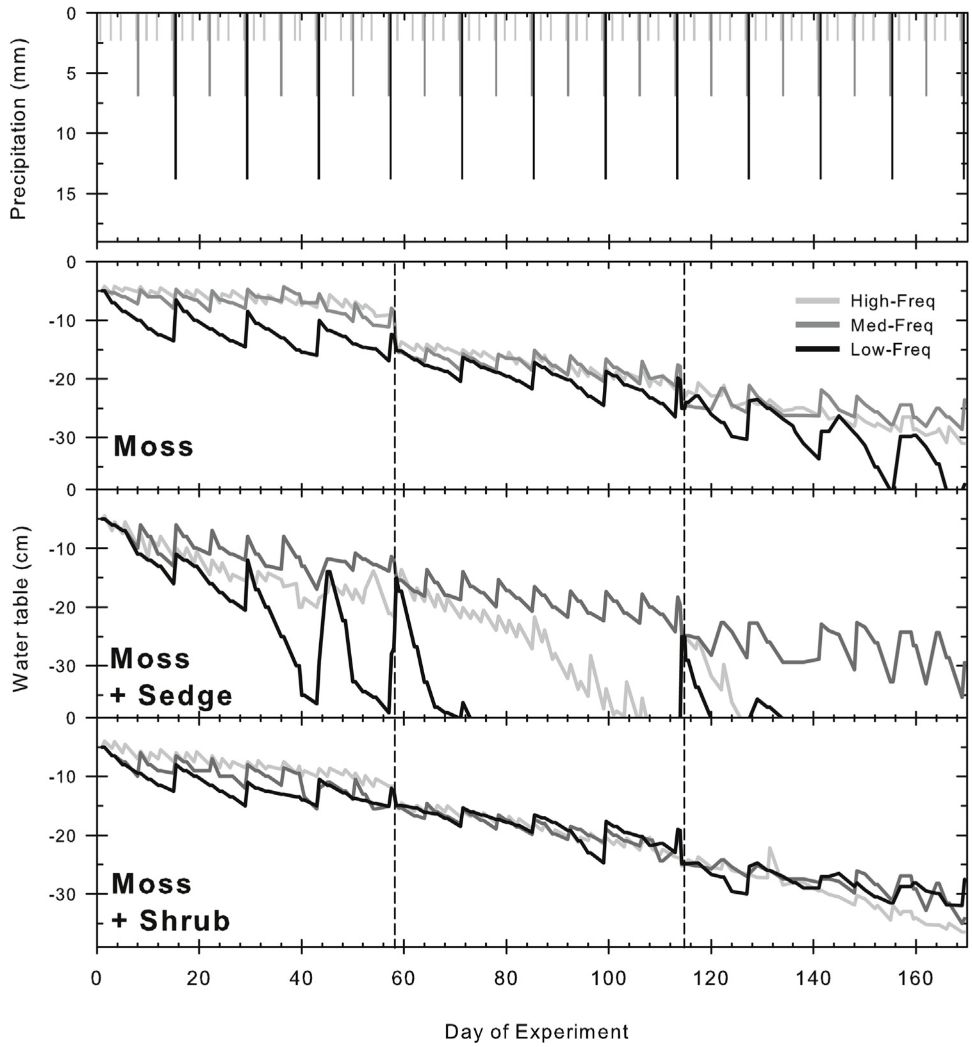

Fig. 5. Water table fluctuation throughout the lab mesocosm experiment. The top panel illustrates the timing and magnitude of the three rainfall treatments, with shading consistent with the water table traces.

occupied ~20% of the surface area of the collars, with *Sphagnum* moss covering the entire basal area, which did not mimic the ~15% moss cover in the shrub-dominated areas of the field. Therefore, while unfortunate, the Moss + Shrub results are consistent with the field and lab Moss treatments, and should not be compared to the field Shrub results.

Our results on the effects of rainfall frequency on peatland CH_4 flux are not directly comparable to previous research investigating prolonged dry periods. Our Low-Frequency treatment simulated a series of short-term (13-day) droughts, with equivalent water being applied after these droughts. Earlier work has focussed on much longer periods without rain. Imposed droughts of between 40 and 100 days have generally led to lower rates of CH_4 production and flux during dry periods (leading to low seasonal fluxes), and following the delivery of large rain events in some instances (Knorr et al., 2008; Knorr and Blodau, 2009; Reiche et al., 2009; Estop-Aragonés et al., 2016). Additionally, it is well established that lower seasonal rainfall and/or increased air temperatures will result in lower seasonal CH_4 fluxes (Nykanen et al., 1998; Strack et al., 2004; Urbanova et al., 2013; Brown et al., 2014). Our imposed 13-day 'drought' was based on recent evidence and plausible climate change projections for the Laurentian Great Lakes region (Emori and Brown, 2005; Cao and Ma, 2009; Walsh et al., 2014), which represents a significant departure from the average 3-day return period of the study site. We also imposed this "drought" whilst maintaining total seasonal rainfall, in alignment with regional climate model projections (IPCC, 2013). Thus, while extended droughts greater than a month, as well as drier than average growing seasons will lead to increased aerobic zones in peat sols and lower seasonal CH_4 fluxes, our data demonstrate the potential for increased CH_4 flux from peatlands subject to a redistribution of atmospheric moisture into low-frequency, high magnitude events that have a high probability of occurring. Current carbon cycle modelling of peatlands have not accounted for this change in moisture regime.

4.2. Role of plant functional types

Through most of the growing season there were no differences in CH_4 flux between the Moss and Sedge plots under the High-Frequency treatment in our field and lab studies; in the latter portion of the season rates were ~60% higher in the Sedge plots relative to the Moss area (Figs. 1 and 2). Decreasing rainfall frequency also had no effect on the CH_4 flux ratio between moss and sedge dominated areas. This is somewhat at odds with previous studies where significantly higher CH_4 flux rates were associated with graminoid vegetation throughout the growing season (Shannon and White, 1994; Waddington et al., 1996; Strack et al., 2006;

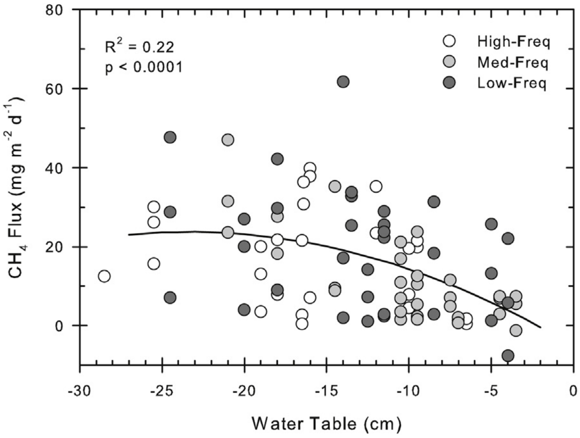

Fig. 6. CH_4 flux in response to water table position for the moss community in the field. Significant relationship is for rainfall treatments combined.

Couwenberg and Fritz, 2012; Ward et al., 2013; Armstrong et al., 2015).

In our study mean flux rates from the *Chaemadaphne calyculata* plots were typically half the rates in the moss and sedge areas. In particular, because the shrub areas were insensitive to decreasing rainfall frequency CH_4 fluxes from Medium- and Low-Frequency treatments were between 1.1 and 7 times less than there comparables in the moss and sedge areas throughout the growing season (Fig. 2). This agrees with previous studies, where it has been suggested that *C. calyculata* and other shrubs lack the aerenchyma development to increase CH_4 transport from the anoxic production zones (Shannon and White, 1994). It has also been suggested that shrubs typically are found in areas with deeper water tables, which serve to limit CH_4 flux due to CH_4 oxidation in the enhanced aerobic surface zone (Bubier, 1995; Armstrong et al., 2015). There were no significant differences in water table depth among shrub-, moss-, or sedge-dominated areas in our field study (Radu, 2017); however, near-surface soil moisture was lower in the shrub areas (unpublished data), which may have enhanced CH_4 oxidation.

4.3. Control of the environmental variables

Because methanogenesis requires reducing conditions most commonly found beneath the water table in peatlands the water table position is generally considered a key control on CH_4 flux (Bellisario et al., 1999; Mahmood and Strack, 2011). In the field experiment water table was found to partially explain the variability in CH_4 flux only in the Moss plots (Fig. 6). The unimodal relationship between water table position and CH_4 flux from the Moss and Moss + Shrub mesocosms for the majority of the low-frequent rain treatments (Fig. 7) has been found previously (Brown et al., 2014). In that study the long-term mean water table position corresponded to maximum CH_4 fluxes. Peak CH_4 fluxes from our columns did occur at water table depths very close to the

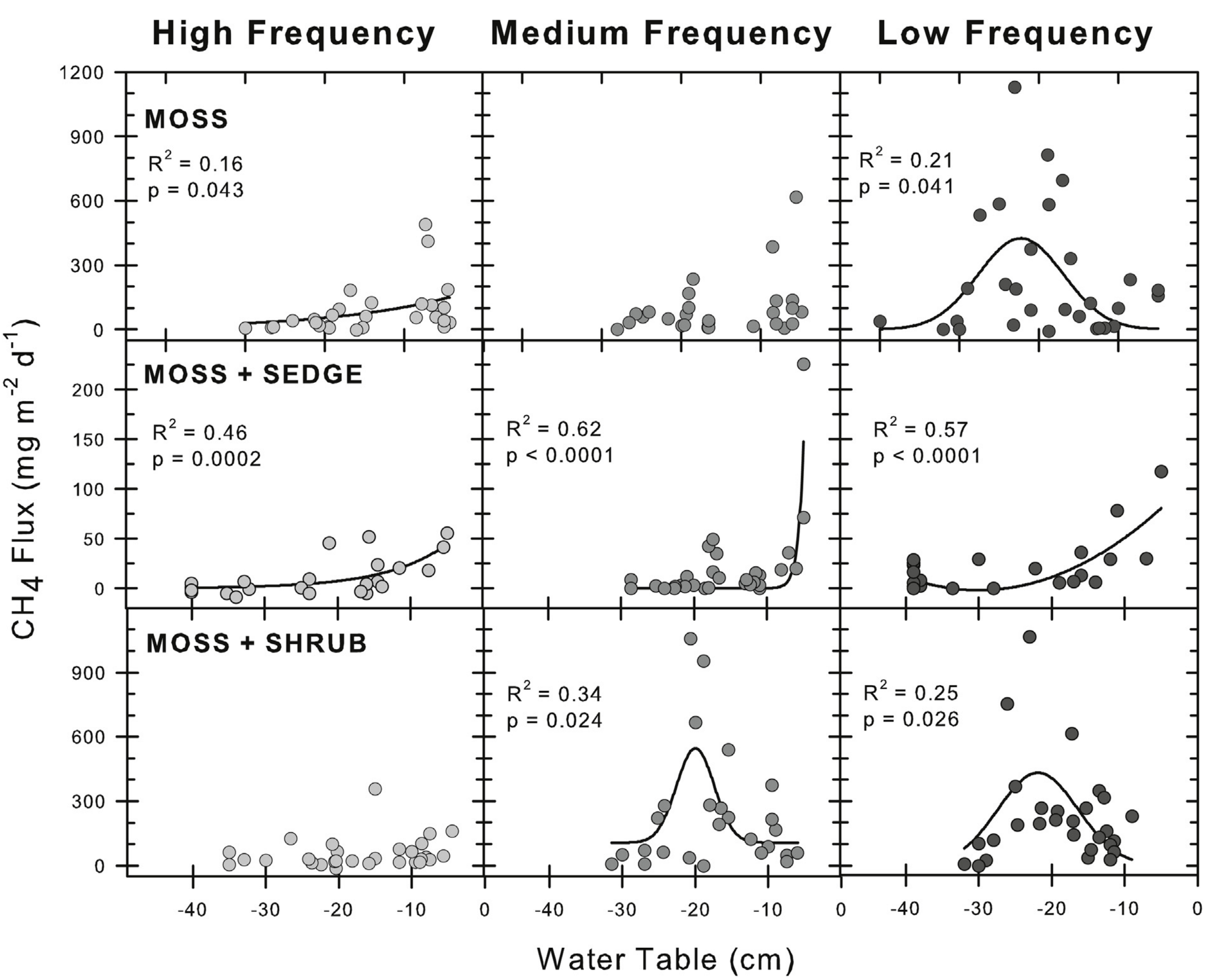

Fig. 7. Relationship between CH_4 flux and water table position from the peat mesocosms for the duration of the experiment, organized by rainfall treatment and vegetation community. Significant relationships are indicated.

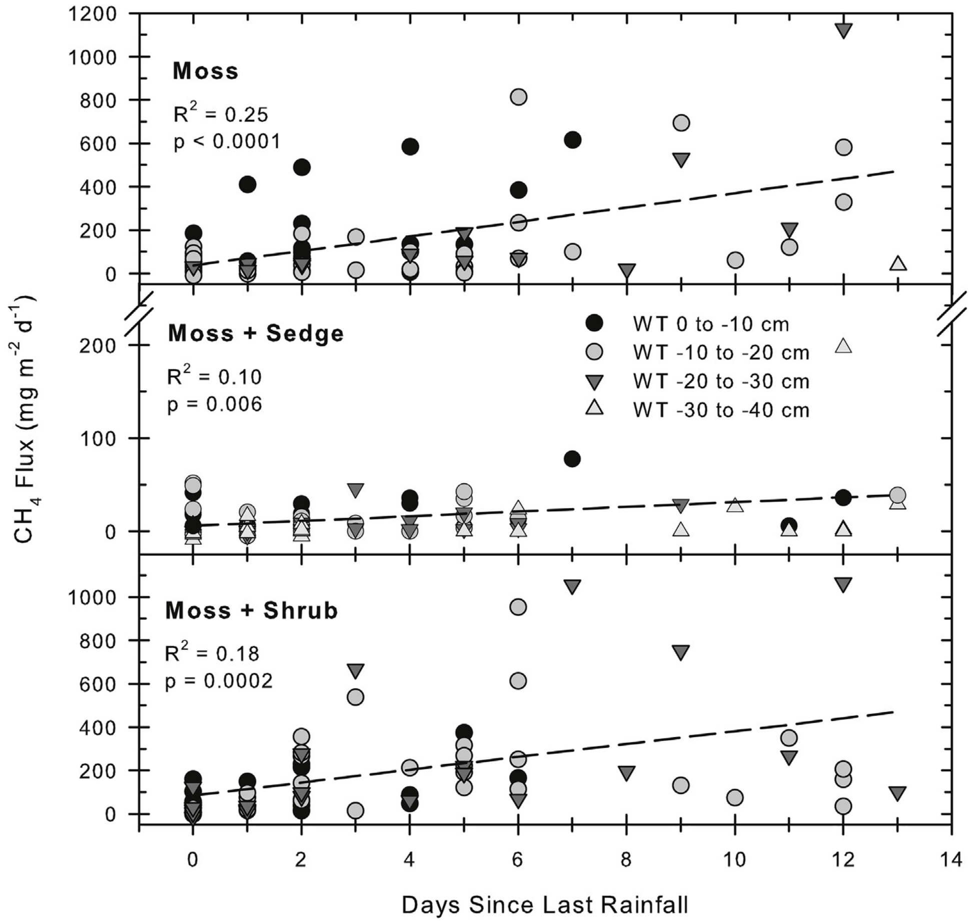

Fig. 8. CH_4 flux from each vegetation community as a function of days since the last irrigation event in the lab mesocosms. Flux data are grouped by corresponding water table position at time of sampling. Linear regression fits and significance are shown for all the data for each vegetation community.

means of the experiment (−20, −18.2, and −18.8 cm for the Moss – Low, Moss + Shrub – Medium, and Moss + Shrub – Low-Frequency factors, respectively). In the field, air temperature was a better predictor in the plots dominated by vascular plants. Air temperature has been shown to be a better predictor of CH_4 flux from peatlands than water table position in a number of studies (Friborg et al., 2000; Sachs et al., 2008; Parmentier et al., 2011; Brown et al., 2014). Aerenchyma formation and vascular transport in the sedges enhances transport from CH_4 production zones to the atmosphere (Knoblauch et al., 2015); increased air temperature increases sedge biomass, enhancing this transport, independent of water table position.

We suggest it is the dynamic water table created by infrequent events that led to greater CH_4 flux from the poor fen in response to the rainfall regime. Moore and Dalva (1993) found significant hysteresis in CH_4 flux from peat soil columns due to their manipulation of the water table, with greater flux while the water table was receding as opposed to rising closer to the surface. With greater duration between wetting events the water table slowly falls (Fig. 5); during this time CH_4 flux remains high in the saturated peat, through increased production and/or degassing from the soils (Dise, 1993; Dinsmore et al., 2009; Estop-Aragones et al., 2016). In the increasing unsaturated zone continued aerobic microbial respiration may accumulate labile substrates. The delivery of a large magnitude event causes a rapid rise in the water table, resetting conditions favourable for lowering redox potential (Knorr et al., 2009) and ultimately renewed methanogenesis (Deppe et al., 2010; Estop-Aragonés et al., 2013). Previous studies have found a long delay of 20–200 days in CH_4 fluxes following rewetting (Shannon and White, 1996; Knorr et al., 2009; Knorr and Blodau, 2009; Reiche et al., 2009; Estop-Aragones et al., 2016); however, in each of those cases the water table was lowered for a significantly longer duration than the present study. It is possible that during a two-week drying period rates of iron and sulphur oxidation do not build up a significant pool of alternative electron acceptors that suppressed methanogenesis in those studies. Thus, while maintenance of high water table position promotes methanogenesis and CH_4 flux in poor fens (Turetsky et al., 2014), the short-term (~14 day) oscillations of the water table due to shifting rainfall regime in this study enhanced CH_4 flux rates in both Moss and Sedge plots. The dynamics of rainfall-induced, water table-mediated optimum conditions for maximum CH_4 flux may explain the unimodal relationship between CH_4 flux and water table position, which in our studied poor fen had a CH_4 flux peak at a mean water table depth of −20 to −24 cm.

4.4. Implications for peatland management

This study has demonstrated a shift in the growing-season rainfall regime to one with numerous short-term droughts punctuated by high-magnitude events will lead to increased water table variability. The increased variability may not be concurrent with a change in mean water table position. Increased water table fluctuation led to increased CH_4 flux in the field from areas dominated by *Sphagnum* moss and *Carex oligosperma* vegetation, but not from areas dominated by ericaceous shrubs such as *Chaemadaphne calyculata*. This has important implications for management of poor fens, given the predicted shifts in the rainfall regime (Kundzewicz

et al., 2006; Trenberth, 2011; IPCC, 2013) and associated changes to peatland water balance, vegetation, and water quality (Cusell et al., 2015; Dorau et al., 2015; Hedwall et al., 2017). Shrub encroachment into fens is of widespread occurrence (Grygoruk et al., 2014) and linked to lower water tables caused by increased temperatures (Weltzin et al., 2003). On the other hand, establishment of sedge species is highly successful in fen restoration and creation (Duval et al., 2010; Vitt et al., 2011; Cooper et al., 2017), increase with increasing water level (Weltzin et al., 2003), as well as with increasing air temperature (Dielman et al., 2014). Thus, fen management activities encouraging sedge prevalence, either through planting activities or increased water levels should expect higher CH_4 fluxes as the summer precipitation regime shifts. Alternatively, one benefit of shrub presence will likely be a net-zero change in CH_4 flux from changing rainfall distribution.

Acknowledgements

We thank the entire Stream and Wetland Ecohydrology Research Group at UTM for their assistance with field setup, collection, and analysis, Brent Coleman and William Ng in particular. We thank two anonymous reviewers whose comments improved this article. This research was funded by NSERC Discovery Grant #418197 to TPD and a NSERC CGS-MS and UTM-Geography GEF to DDR.

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